

Microhabitat Segregation of Three Species of Pocket Mice (Genus *Chaetodipus*) in Coastal Baja California, Mexico

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Abstract.—I compared vegetation and substrate characteristics at capture locations of three syntopic species of pocket mice (*Chaetodipus*: Heteromyidae) to determine differences in microhabitat affinities of these ecologically similar rodents in coastal Baja California, México. Principal components analysis revealed that capture locations of *C. spinatus* had disproportionately higher cover of medium and large rocks, and tended to have higher plant species diversity than capture locations of the other two species. *C. spinatus* and *C. arenarius*, the two smallest species, differed most in their microhabitat affinities, suggesting spatial segregation that may minimize competition for similar food resources. *C. arenarius* was captured most often at sites with the finest-textured soils, whereas *C. rudinoris*, the largest species, was widespread and frequently associated with gravel and small rocks. No species showed any apparent preference for plant species or significant amounts of overhead cover, a conclusion supported by the high densities of *C. rudinoris* on small, barren islands in the Gulf nearby. My results represent the first quantitative descriptions of the habitat associations of these species, which are wholly or predominantly restricted in their distributions to Baja California.

Studies of desert rodents have provided important insights into the mechanisms that permit species coexistence (Kotler and Brown 1988; Brown and Harney 1993). Desert rodent communities are often incredibly diverse, containing as many as 14 species, and in the case of North American deserts, are dominated by granivorous heteromyids (Brown and Harney 1993). The co-occurrence of multiple, ecologically similar heteromyid species has been attributed to subtle differences in diet (e.g., Brown and Leiberman 1973; M'Closkey 1978), foraging efficiency (Price and Heinz 1984; Price and Waser 1985; Brown 1989), predator escape abilities (Kotler 1984; Longland and Price 1991) and body size (Bowers and Brown 1982), all of which reflect the long-term consequences of competition, predation risk and biogeographical history (Brown and Harney 1993). These differences usually are manifest in patterns of microhabitat use (e.g., Price 1978; Wondolleck 1978; Thompson 1982), with species separated locally in space by the amount and species composition of plant cover and soil and substrate characteristics (Reichman and Price 1993).

As part of a study of the ecology of coastal and insular populations of rodents in northern Baja California, I captured three species of pocket mice (*Chaetodipus arenarius*, *C. rudinoris* and *C. spinatus*) in very close proximity to one another, at locations with seemingly similar vegetation and substrate features. I recorded microhabitat characteristics at capture locations of each species to look for evi-

dence of microhabitat partitioning that might explain the co-occurrence of these otherwise ecologically similar species, which comprise approximately 75% of captures of rodents in the study area (Stapp and Polis 2003). These species have their distributions either wholly (*C. arenarius*) or predominantly (*C. spinatus*, *C. rudinoris*) in Baja California (Lackey 1991a, b; Paulson 1988), yet little is known of their ecology outside of the general habitat descriptions provided in taxonomic references (e.g., Burt 1932; Huey 1964). Riddle et al. (2000) recently proposed that populations of *C. baileyi* west of the Colorado River are a distinct species, *C. rudinoris*. To my knowledge, this study provides the first quantitative descriptions of the habitat affinities of these species.

Methods

The study was conducted from May–October 1998 in a wide desert bajada located 10 km north of Bahía de los Angeles, along the Gulf coast of Baja California, México. Vegetation is Sonoran desert scrub and dominated by perennial shrubs (*Bursera hindsiana*, *B. microphylla*, *Fouquieria* spp., *Lycium* spp., *Larrea tridentata*, *Jatropha cuneata*), short trees (*Olneya tesota*, *Pachycormus discolor*, *Cercidium microphyllum*) and cardons (*Pachycereus pringlei*). *Frankenia palmeri*, *Suaeda moquinii* and *Salicornia subterminalis* are the dominant plants in a narrow zone of fine-textured soil 50–75 m from the shore. The beaches adjacent to the study area were covered with smooth cobble. Annual plants were abundant inland in the spring of 1998, following a strong 1997–98 El Niño Southern Oscillation event that brought 440 mm of rain to the area, which normally receives <59 mm annually (Stapp and Polis 2003).

In May 1998, I established two 1.5-ha trapping grids, separated by approximately 1 km. Grids consisted of 54 trap stations, with six parallel transects originating in the supralittoral zone and extending inland perpendicular to the shore for 200 m. Transects were 15 m apart and consisted of nine stations spaced at 25-m intervals. Each trap station had a single Sherman live trap, which was baited with peanut butter and oats. The size of the grid was reduced to four transects in October 1998 (36 traps; 0.9 ha).

Rodents were live-trapped for three consecutive nights in May and October 1998, but because feral dogs disturbed many traps on the third night, I used only data from two nights of trapping in each session to estimate species composition and relative abundance. Traps were opened at dusk and checked and closed at dawn each morning to prevent heat-induced mortality. Each individual captured was measured, weighed and given a uniquely numbered aluminum ear tag. All individuals were released at their capture location. I used the number of individuals captured per unit trapping effort as an index of relative abundance.

Vegetation and substrate characteristics were recorded within a 3-m radius plot of each trap station where different *Chaetodipus* were captured, omitting recaptures of the same individual at the same station. I recorded the number of species of trees (≥ 2 m in height), shrubs, and ground cover plants (mostly annuals), and estimated visually the percentage canopy cover of plants in the plot. I characterized the percentage cover of each type of substrate within each plot, using the following categories: sand; marine silt; small rocks (ca. 2–10 cm diameter); medium rocks (10–30 cm); large rocks (>30 cm). Another observer and I estimated percentage cover of plants and substrate independently, and the mean of these

Table 1. Relative abundance [number of individuals/100 trap-nights (TN)] of rodents on two, 1.5-ha coastal study areas near Bahía de los Angeles, Baja California, México in 1998. The number of unique trap stations used denotes the number of different trap stations where each species was captured. Mean abundance was calculated for May and October trap sessions on each site; values presented are the means \pm 1 s.e. of the two study areas. For comparison, 44% of all trap stations were \leq 75 m from shore. Body weights are means \pm 1 s.e., with n in parentheses, based on live-trapping on the mainland between 1997–2001 (P. Stapp, unpubl. data).

Species	Adult body weight (g)	No. individuals (total captures)	Relative abundance (No./100TN)	No. of unique trap stations used	Percent of capture locations \leq 75 m from shore
<i>Chaetodipus rudinoris</i>	19.5 \pm 0.4 (59)	49 (59)	14.34 \pm 4.69	42	40.48
<i>Chaetodipus spinatus</i>	15.0 \pm 0.3 (50)	42 (43)	14.69 \pm 1.25	34	17.65
<i>Chaetodipus arenarius</i>	11.2 \pm 0.1 (25)	16 (17)	5.23 \pm 0.01	16	50.00
<i>Dipodomys merriami</i>	34.2 \pm 1.0 (18)	16 (19)	5.57 \pm 3.11	14	57.14
<i>Peromyscus eremicus</i>	16.2 \pm 0.5 (17)	7 (8)	2.72 \pm 0.30	8	37.50
<i>Neotoma lepida</i>	131.8 \pm 7.5 (10)	7 (9)	2.24 \pm 0.26	7	85.71

estimates was used in data analysis. Principal components analysis was used to reduce the number of correlated variables for comparisons of differences in microhabitat associations of each species. Within each plot, I also recorded presence of mounds with extensive burrow systems to evaluate the efficacy of using these burrow networks as an indicator of species presence.

Results

Six rodent species were captured on both study sites (Table 1). As in other Sonoran Desert communities, heteromyids were numerically dominant. Sigmodontine rodents (*Peromyscus eremicus*, *Neotoma lepida*) were captured only occasionally and represented by few individuals. *Chaetodipus spinatus* and *C. rudinoris* were most abundant and captured in approximately equal numbers, whereas *C. arenarius* and *Dipodomys merriami* were less common. Although all species except *D. merriami* were captured in traps in the supralittoral zone, *C. spinatus* was largely restricted to scrub vegetation far from shore (Table 1). In contrast, *C. rudinoris* and *C. arenarius* were dispersed fairly uniformly across the trapping areas. *N. lepida*, an herbivorous species typically associated with rocky slopes and outcrops, was restricted primarily to the dense *Salicornia* and *Suaeda* cover near shore (Table 1). *C. formosus* is known to be present in the area (Stapp 2002; G. Stewart, pers. comm.), but was not caught on the study sites during my study.

Analysis of microhabitat variables at capture locations suggested differences among species in their affinities for local substrate and soil characteristics. Four principal components had eigenvalues $>$ 1.0, with the first principal component axis (PC1) accounting for nearly 28% of the variance (Table 2). The three species differed only in their scores for PC1 (Kruskal-Wallis test, $\chi^2 = 9.20$, d.f. = 2, $P = 0.01$; all other PC axes, $P > 0.19$). Capture stations of *C. spinatus* had significantly higher mean scores for PC1 (mean \pm 1 s.e. = 0.65 ± 0.25) than those where *C. rudinoris* (-0.33 ± 0.21) and *C. arenarius* (-0.52 ± 0.31) were caught. Based on the correlations between microhabitat variables and PC1 (Table 2), capture locations of *C. spinatus* were significantly more rocky (i.e., had proportion-

Table 2. Microhabitat characteristics (mean \pm 1 s.e.) of capture locations of three species of *Chaetodipus* near Bahía de los Angeles, Baja California, México. Sample size is the number of unique trap stations used by each species (Table 1). The major plant species listed were those present at $\geq 20\%$ of capture locations of a given species. The last four columns are correlations between four principal components with eigenvalues >1.0 and variables describing vegetation and substrate characteristics.

Microhabitat variable	PC correlations			
	<i>C. ruidinoris</i>	<i>C. spinatus</i>	<i>C. arenarius</i>	
No. tree species	0.40 \pm 0.11	0.50 \pm 0.11	0.31 \pm 0.12	PC1 0.42
No. shrub species	1.88 \pm 0.17	2.12 \pm 0.23	1.88 \pm 0.26	PC2 0.26
No. understory species	3.10 \pm 0.36	3.91 \pm 0.27	2.88 \pm 0.50	PC3 -0.22
% plant cover	27.07 \pm 2.79	21.12 \pm 3.08	30.94 \pm 4.94	PC4 -0.16
% sand or silt	68.81 \pm 5.11	58.53 \pm 5.42	78.75 \pm 5.82	0.36
% small rock	23.33 \pm 4.64	15.88 \pm 4.59	11.56 \pm 4.13	0.40
% medium rock	3.69 \pm 8.77	22.35 \pm 4.85	5.94 \pm 2.75	-0.60
% large rock	4.17 \pm 2.09	3.09 \pm 1.12	2.19 \pm 1.51	0.12
Major tree species ^a	PADI, FOSP, BUHI	PADI, FOSP, BUHI, OLTE	PADI, FOSP, BUMI, CEMI, PAPR	0.15
Major shrub species ^b	FRPA, LYCI, LATR, SUMO, SASU	LYCI, LATR, JACU, VIGE	FRPA, LYCI, LATR, BUMI, JACU	0.49
Major understory species ^c	PEEM, ARAD, EUPH, DAES, MAEV	PEEM, ARAD, EUPH, DASE, MAEV	PEEM, ARAD, EUPH, MAEV	-0.41
Eigenvalue				2.21
% variance explained				1.79
				1.32
				27.63
				16.51
				14.06

^a PADI, *Pachycormus discolor*; FOSP, *Fouquieria* spp.; BUMI, *Bursera hindsiana*; BUMI, *Bursera microphylla*; OLTE, *Olmeya tesota*; CEMI, *Cercidium microphyllum*; PAPR, *Pachycereus pringlei*.

^b FRPA, *Frankenia palmeri*; LYCI, *Lycium* spp.; LATR, *Larrea tridentata*; SUMO, *Suaeda moquini*; SASU, *Salicornia subterminalis*; JACU, *Jatropha cuneata*; VIGE, *Viscainoa geniculata*.

^c PEEM, *Perityle emoryi*; ARAD, *Aristida adscensionis*; EUPH, *Euphorbia* spp.; DASE, *Dalea seemanii*; MAEV, *Marina evanescens*.

ately less fine-textured soil) and tended to have overall higher plant species diversity than those of the other two species. This interpretation is supported by inspection of the mean values of the microhabitat variables separately (Table 2). However, capture locations of the three species tended to be dominated by the same plant species. The presence of *Frankenia*, *Suaeda* and *Salicornia* at capture locations of *C. rudinoris* and, to a lesser extent, *C. arenarius*, reflected the frequent captures of these species in coastal vegetation.

The degree of overlap among captures of the three *Chaetodipus* species provides additional evidence of differential microhabitat use by the two smallest (and presumably, most similar ecologically) species. *C. rudinoris* and *C. spinatus* were often captured at the same trap (36% and 44% of *C. rudinoris* and *C. spinatus* captures overlapped, respectively), but *C. spinatus* rarely overlapped with the smaller *C. arenarius* (12% and 25% of *C. spinatus* and *C. arenarius* captures, respectively). In inland areas where *C. spinatus* was most abundant, *C. arenarius* was restricted to the sandy bottoms of dry washes.

Mounds with extensive burrow networks were present at 26–35% of capture locations of *Chaetodipus*, which implies that the presence of mounds is not a reliable indicator of trap success. Capture locations with these mounds were always associated with *C. spinatus* or *C. rudinoris*, and mounds were present at several locations where only one of these species was captured, suggesting that both build mounds. In contrast, all *C. arenarius* capture locations with mounds were trap stations where other species were also captured, suggesting that *C. arenarius* does not construct these mounds.

Discussion

Three species of pocket mice were captured in close proximity to one another, and often, at the same locations, in two trapping areas in coastal Baja California. There were no obvious differences among species in plant cover or species composition at capture locations, although areas inhabited by *C. spinatus* tended to have higher overall plant diversity than capture locations of the other two species. All species were captured frequently in locations with little overhead cover (>50% of capture locations had <20% plant cover). The two smallest species differed primarily in their preference for different substrates, with *C. arenarius* being restricted to the finest-textured soils, and *C. spinatus* associated with a mixture of substrates that included more medium and large rocks. *C. rudinoris*, the largest pocket mouse locally (Table 1), was also the most widespread, and was clearly more generalized in its microhabitat affinities. Both *C. rudinoris* and *C. arenarius* were captured frequently in coastal vegetation, the latter in sand and fine marine silt, and the former in areas with gravel and small stones. The ability of *C. rudinoris* to use gravelly substrates has been reported previously for the closely related *C. baileyi* (Rosenzweig and Winakur 1969; Price 1978; Wondolleck 1978), and may explain the persistence of *C. rudinoris* on small (<0.2 km² area) islands just offshore (Lawlor et al. 2002). Although islands in Bahía de los Angeles are extremely rocky and sparsely vegetated, *C. rudinoris* maintains high population densities on these islands (Stapp and Polis 2003).

Interspecific differences in substrate affinities may reflect differences in relative foraging efficiencies of the three species, as well as variation in the number and size distribution of seeds among microhabitats (Reichman 1984). Unfortunately,

these data are lacking for my study area and the three species I studied. Laboratory experiments (Price and Heinz 1984) suggested that heteromyids, regardless of size and morphology, forage most efficiently when seed densities are high and soils are sandy. However, *C. baileyi*, the close congener of *C. rudinoris*, and *Perognathus amplus*, which is similar in size and morphology to *C. arenarius* (Table 1; Price and Heinz 1984), differed in their preferences for soil texture, with *C. baileyi* preferring coarse soils and *P. amplus* extracting more seeds from fine-textured soils (Price and Waser 1985). In my study, *C. arenarius* and *C. rudinoris* seemed to overlap in their microhabitat associations, but they may select soil characteristics on a finer scale than could be detected by my sampling methods. However, given the large difference in body size (9 g; Table 1) between these two species, they may also have distinct preferences for different sizes or spatial distribution of seeds that may explain their co-occurrence. More information on the density and accessibility of seeds in rocky substrates, on the foraging behavior of *C. spinatus*, and on possible competitive effects of *C. rudinoris* on the smaller pocket mice is needed to assess patterns of spatial overlap in this system.

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